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ABNORMALITIES IN OENOTHERA.

BY R. R. GATES.

In connection with my *Oenothera* cultures, particularly among plants grown during the past two seasons at the Missouri Botanical Garden, I have had occasion to observe several interesting "abnormalities" of structure. These include virescence or frondescence and polymery of the flowers, tricotyly and variegation of leaves. I have thought it worth while to devote a short paper to a description of some of these cases which have an evident bearing on problems of variation and inheritance.

VIRESCENCE.—In my experimental garden of 1909 four plants exhibited virescence of the flowers. These were all descendants in the second generation from plants which were derived from the English coast near Liverpool, the first generation having been grown at Woods Hole, except in the case of one (No. 47), which was grown in the tropical greenhouse at the University of Chicago. These four plants were therefore all from cultures of closely related forms, and in some of their characters were intermediates between *O. grandiflora* and *O. Lamarckiana.* The summer temperature at St. Louis in 1909 ranged exceptionally high, reading 100° F. in the shade in one instance. The change in climate which the plants experienced was therefore very considerable, and one of the cultures had been subjected to such high temperatures for two successive seasons. This may perhaps have had something to do with the appearance of these cases of virescence, the alteration in the conditions acting as a stimulus to the production of the abnormality. That the tendency to produce virescent individuals is inherited, is shown by the reappearance of virescent plants in one race in successive generations, and their failure to appear in many other races, *e. g.*, *O. Lamarckiana* and its mutants.

Two of the cases of virescence in 1909 occurred in a race which I have called *O. multiflora,* the description of which will be published at another time. This race is descended from a single individual grown at Woods Hole in 1908. A total of 376 first-generation offspring of this individual have been grown in the two following years, and also (in 1910) 50 plants of the second generation from the self-pollination of one individual of the first generation. The plants of the F_1 included a total of 15 virescent individuals, or very nearly 4%. The 50 plants of the F_2 contained one showing virescence. In a culture of 36 plants from seeds received from the Botanical Garden at Karlsruhe under the name *O. chilensis,* which proved to contain two very distinct types, one plant was virescent. This abnormality has not appeared in any others of the many races of which I have grown cultures.

All the plants showing virescence were affected in exactly the same way, although in some the early flowers were normal and produced fruits, only the later flowers showing the peculiarity. I have not compared the offspring from such capsules with those of normal plants, though if this were done it might be found that the virescent tendency was inherited more strongly in the former case. In one plant a side shoot produced flowers which were quite normal while the main stem produced only flowers of the virescent type.

One plant of *O. multiflora,* in which all the flowers but the earliest were virescent, is illustrated in plate 29. The peculiarities of structure exhibited by these flowers may now be described. Plate 30, f. 1, shows a group of the flowers, natural size. The sepals are green inside and outside, large and bag-like and more or less crinkled or curled. They are tapering at the end, terminating in long, slender sepal tips. Perhaps frondescence or phyllody would be a more suitable term than virescence to apply to this condition, for the sepals have become quite leaf-like. Plate 30, f. 2, shows several flowers opened and photographed to show the other organs of the flower. The petals retain a greenish yellow color, but are in all cases very small (usually about half an inch in length, though sometimes larger) and blunt at the tip. The anthers are small, with very short filaments, empty and sterile. The style is frequently markedly pubescent almost to the top. It tapers strongly and gradually to the top which is very slender, and the stigma lobes are reduced to four delicate prongs.

A remarkable peculiarity of all these flowers is the complete, or almost complete, suppression of the hypanthium. I have remarked elsewhere (Gates, 1910, footnote, p. 208) that the attacks of a certain insect also lead to suppression of this organ. Its wide variability, which Shull (1907) has proved statistically, and its suppression under various abnormal conditions, as I have shown, are probably significant facts, related to its recent phylogenetic development as suggested by MacDougal. A marked feature of this type of virescence is that the flowers do not drop off but remain permanently attached to the stem. In many cases an elongation occurs below the ovary. This is more slender than the ovary and is hard and woody, tough, and strongly attached to the stem. In the meantime (see plate 30, f. 2, flowers to the left) leaves grow out from the interior of the flower and in this way the flower becomes transformed into a short side branch. The ovary in the meantime almost completely disappears, possibly becoming transformed into a portion of the woody branch by an alteration in its structure. This stem is always more slender than was the original ovary. A whole group of young leaves of abnormal shape (long and narrow) may grow out of the flower in this manner. The elongation to form a side branch is sometimes partly above and partly below the ovary, as may be seen from plate 29. It may also be seen from this figure, though not clearly, that the lower flowers on the main stem were normal and have dropped off leaving the growing ovaries behind. Some of these afterward developed into large capsules.

The plant in 1909 which produced only virescent flowers, wilted and died about August 10th for no assignable cause, while the other plants continued to bloom long afterwards. It seemed as though the production of virescent flowers was equivalent to seed production in the physiology of the plant, and was therefore followed by drying up and death such as occurs with normal plants later in the season. The plant in the offspring of No. 47, showing virescence, was not observed to have virescent flowers until September 29, when the blooming season was nearly past. On this plant the ends of all the branches bore only virescent flowers, while farther down the branches normal seed capsules had been produced. Virescence therefore developd in all the flowers simultaneously but only appeared at the end of the season. The virescent flowers on this plant became fairly stout branches, in some cases even possessing internodes.

In the virescent flowers there was no departure from the normal number of parts, but when leaves developed within these they exhibited no regularity in number or arrangement, though always growing out from just within the cycle of the petals.

DeVries refers to what appears to be a similar case in *Oenothera subovata* (1909, p. 423), but does not describe it. He has also described a different type of virescence which is pathological in nature, due to the attacks of certain parasites. Masters (1869) gives a list of cases of virescence (p. 338) in which he includes Oenothera, with the suggestion that it might perhaps better be called frondescence or phyllody. On p. 252 of the work referred to, cases of frondescence or virescence of petals in *Oenothera striata* are cited.

POLYMERY OF THE FLOWERS.—A number of cases of flowers with an increased number of parts were observed in the cultures of 1909 and 1910. No special effort was made to find them all, but they were recorded as they happened to be observed by myself or my assistant. Masters, on p. 44 of the work above cited, refers to species of Oenothera as exhibiting synanthy. Many of the cases of polyphylly in flowers of Oenothera, to be described shortly, are due to synanthy, as I shall show. Certain other cases will require a different explanation.

DeVries (1909, pp. 472, 482) has recorded a number of cases of polymery from his cultures and in the field at

Hilversum. I will add some observations which extend the range of variation in number of parts, and shall then suggest what appears to me a probable explanation of the phenomenon as it occurs in most of the races of Oenothera. All the cases in 1909, with the exception of two, occurred in hybrid *O. Lamarckiana* from various sources, and these two were *O. brevistylis* plants from a cross with *O. Lamarckiana.* Whether this is of significance as indicating greater variability in plants derived from a cross, I cannot say, but it seems not improbable that this is the case. Using signs for the flower parts I shall now give the formulæ for the flowers recorded in 1909, in which K=sepal, C=petal, S=stamen, N=stigma lobe.

1.	$K_7C_?S_{15}N_{13}$	6.	$K_5C_5S_{10}N$
2.	$K_6C_6S_{12}N_{11}$	7.	$K_6C_6S_{12}N_9$
3.	$K_7C_7S_{16}N_{13}$	8.	$K_7C_7S_{14}N_9$
4.	$K_5+C_7S_{14}N_{12}$	9.	$K_7C_7S_{16}N_{7+5}$[1]
5.	$K_3C_3S_6N$	10.	$K_3C_3S_6N$
11.	$K_3C_3S_6N$		

This list of flowers, while shorter than that of DeVries, extends in both directions the range of variations observed by him. The highest number of stamens recorded by DeVries in a flower is 14, while I observed one remarkable flower with 16 stamens and two styles which were separate at the top, in contact below, but terete and easily pulled apart. The hypanthium was also considerably flattened and much thicker than usual and even had a longitudinal groove down its center. This flower gave me the clue to the explanation of these cases of polymery.

DeVries states (1909, p. 483) in regard to his cultures of *O. Lamarckiana* forms, that "trimerous flowers are certainly not present," but he has observed them, though very rarely, in *O. biennis* and in hybrid cultures. In the season of 1909 I observed three such cases, in *O. Lamarckiana* of various descent. The flowers were normal in every way except that the parts were in threes, which made the flowers smaller, though the individual organs were not reduced in size.

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[1] This flower had two independent stigmas, and styles which were merely in contact in the calyx tube.

Regarding the explanation of these cases, I soon found that every polymerous flower had two bracts at its base instead of being in the axil of a single bract. These bracts may be entirely independent or they may be more or less coalesced at the base, but they project in opposite directions. (See photograph by DeVries, 1909, p. 472.) In all these cases the ovary and hypanthium are more or less flattened. An examination of the stems which bore these polymerous flowers, disclosed the fact that they exhibited irregularity in the placing of the flowers on the stem, or in other words, variations in phyllotaxy. The flowers and their bracts were not uniformly distributed on the stem, but certain flowers were very close together and others long distances apart. It seems clear that this is the explanation of the phenomenon, which is therefore one of synanthy rather than of polymery. The Anlagen of the flowers are of course laid down and their position determined when the terminal rosette of the stem is very small. Anlagen of successive flowers therefore arise very close together, and if anything leads to variation in their position they will sometimes occur partly in contact or overlapping, giving a flower in which the parts are more or less completely doubled in number. The flower having two independent styles, and the fact that two bracts are always found at the base of polymerous flowers, shows that it must be due to a partial coalescence of primordia, such as I have mentioned. It is interesting to note that flower No. 5, having its parts in threes, was immediately below No. 4, which is heptamerous, and on the same side of the stem. Similarly, the plant bearing flower No. 9 also bore at the same time (Aug. 20) the two trimerous flowers, Nos. 10 and 11. It may also be noticed that in all the polymerous flowers the number of stigma lobes is less than the number of stamens. The same is true of DeVries' records. These polymerous flowers are much larger than the normal owing to the larger number of parts, the parts themselves retaining their usual size, except that the hypanthium and style are stouter, as might be expected, and the filaments are sometimes thicker.

In the season of 1910 a number of additional observations were made on this subject. The records of these were kept by my assistant, Mr. V. Follenius, during my absence, but I had the opportunity of examining the most interesting cases before the end of the season. Cases of polyphylly or synanthy were found in a much wider range of Oenothera forms than in the previous year. The following is the list:

FORMULA	RACE	REMARKS
1..$K_7C_7S_{14}N_{11}$	*O. multiflora*	Two bracts at base of flower.
2..$K_6C_6S_{12}N_8$	*O. multiflora*	Two bracts partly coalesced.
3..$K_6C_6S_{12}N_8$	*O. multiflora*	Two bracts at base.
4..$K_4C_4S_8N_4$ $K_4C_4S_8N_5$	Race No. 25, from near Liverpool, England	Two perfect tetramerous flowers, with their hypanthia in contact throughout their length and partly fused. Ovaries in contact and partly fused. Two bracts.
5..$K_3C_3S_6N_6$	*O. biennis* × *Lamarckiana*	One bract.
6..$K_3C_3S_6N_4$	" "	One bract.
7..$K_3C_3S_8N_5$	" "(same plant as No. 6)	One bract.
8..$K_6C_6S_{12}N_8$	*O. grandiflora* from Alabama	Hypanthium and ovary flattened. *One* bract.
9..$K_5C_5S_?N_?$	Race 54 × 40	*One* bract.
10..$K_5C_5S_8N_8$	*O. biennis*, Chelsea Physic Garden	Only *one* bract at base of each flower in this race. In one case the bract had two tips, as though resulting from the incomplete coalescence of two bracts.
11..$K_5C_5S_8N_8$	" "	
12..$K_5C_5S_8N_8$	" "	
13..$K_5C_5S_8N_7$	" "	
14..$K_5C_5S_8N_5$	" "	
15..$K_5C_5S_8N_5$	" "	
16..$K_5C_5S_8N_5$	" "	
17..$K_5C_5S_8N_5$	" "	
18..$K_5C_5S_8N_5$	" "	
19..$K_5{}^1C_4S_9N_4$	" "	[1] Two sepals of normal width, 3 narrower, occupying about the width of the other two.

The case of No. 4, in which two tetramerous flowers were found, each with its bract, and only partly fused by their ovaries and hypanthia, is particularly instructive and confirmatory of my explanation. One hexamerous (No. 8) and one pentamerous (No. 9) flower, however, had each but *one* bract at its base, as well as the three trimerous flowers in the race *O. biennis* × *O. Lamarckiana*. It is therefore probable that the latter are real cases of polyphylly and not of synanthy, in which, instead of the partial coalescence of two primordia or their failure to separate, there is a variation in the division of the Anlagen of the various cycles of organs in the flower, resulting in a flower having a larger or smaller number of parts than normal. When, as in flowers 10–18, the androecium is normal while the calyx and corolla show an increase of parts, this may be considered to be due to polyphylly rather than synanthy.

The ten pentamerous flowers in *O. biennis* from the Chelsea Physic Garden were found in a culture of 33 plants, and careful search would doubtless have revealed further cases. Evidently the phenomenon is relatively common in this race.[1] The characters of the race are very constant and are remarkably different from those of any other race of *O. biennis* I have seen. They will be described elsewhere. These pentamerous flowers had invariably but one bract at their base, which would indicate that the phenomenon of pentamery is here due to polyphylly rather than to synanthy, although the fact that one of these basal bracts had a double tip might be considered to favor the interpretation of this also as due to synanthy.

It would seem therefore that while most of these are cases of synanthy, or coalescence of two primordia, the trimerous flowers and also evidently some at least of the other cases with only one bract at base, are real instances of polyphylly, due to variations in the divisions which the primordia of a flower normally undergo.

My conception of the process of synanthy is that, owing to variations in phyllotaxy, two independent flower primordia become so closely approximated that they partly coalesce, and develop harmoniously into a single flower in a somewhat similar fashion to the growth of a plant chimera (sectorial chimera) as described by Baur and by Winkler.

TRICOTYLY.—A number of cases of tricotyly and other abnormalities of the cotyledons have been observed in my germinating pots each year. They are particularly common in *O. gigas,* but no record of them has been kept.

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[1] Penzig (1890) states that in *O. biennis* pentamerous flowers are common, the number of "carpels" often running up to 9.

Variegation of Leaves.—Yellowish areas not infrequently appear on the rosette leaves, particularly in the English Oenotheras. One striking case of what was evidently a sectorial chimera according to Baur's (1909) terminology, occurred in a culture of 55 plants very closely resembling *O. Lamarckiana,* but having larger rosettes with rather broader leaves. They constituted the second pure generation from seeds of a plant near Liverpool, England. The green areas on the leaves in this plant are contrasted with areas which are yellowish white, showing a complete absence of chloroplasts. It will be seen that in several leaves the line between white and green tissue passes down the midrib, while one or two leaves exhibit patches of white adjoining the midrib. Plate 31, from a photograph taken June 30, 1909, shows the partly developed rosette. The leaves arising from one side of the stem are wholly white, those on the opposite side are mostly pure green, while several others are green on one-half and white on the other. A few areas of pale green, owing to partial absence of chlorophyll, were also observed. The white areas were of course unable to nourish themselves, and continually died away. The plant never formed a shoot, but died before the end of summer, notwithstanding the most careful treatment. The plants of the previous generation gave no indication of such a condition, which therefore appeared suddenly in this individual, and appeared, moreover, from a seed of a plant which was normal green throughout. Presumably one side of the young growing point was without chloroplasts, but just how this condition came about is at present a matter of conjecture.

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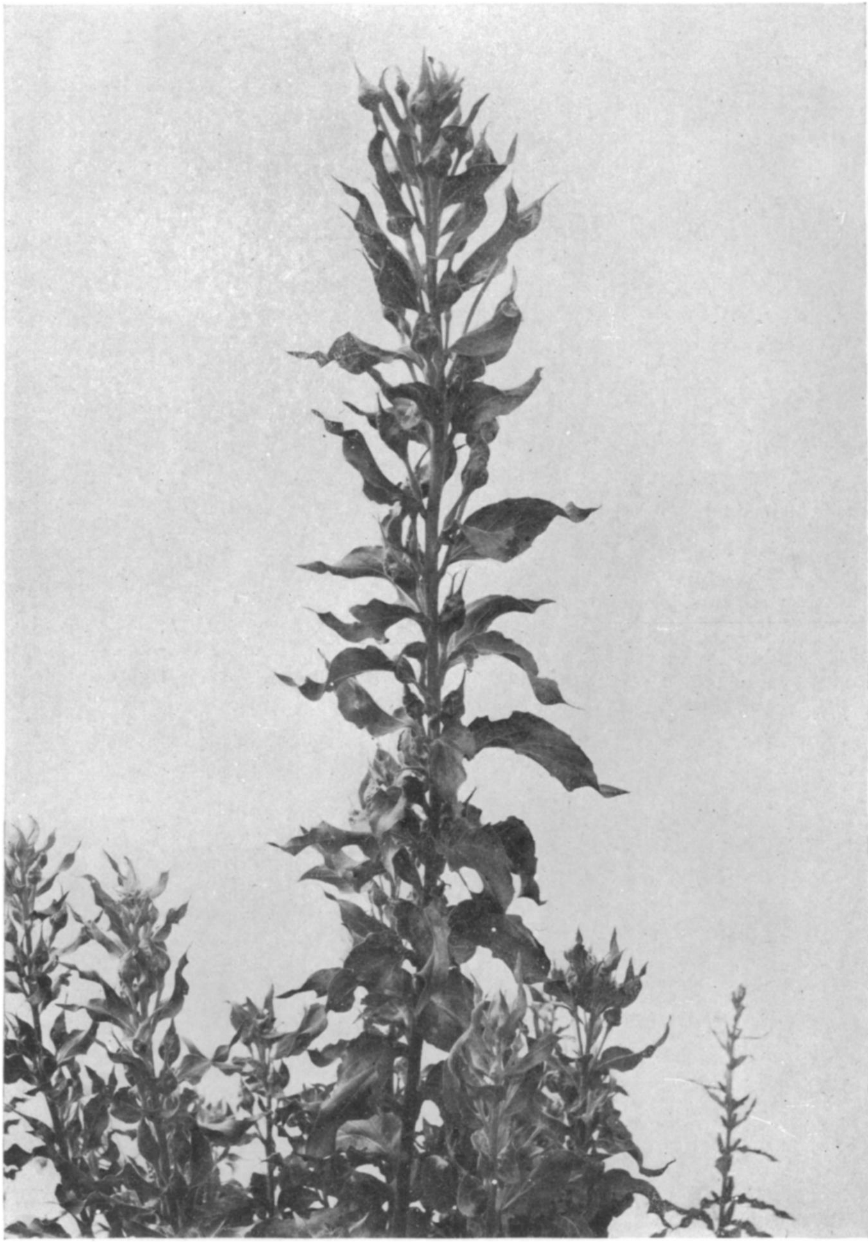
EXPLANATION OF PLATES.

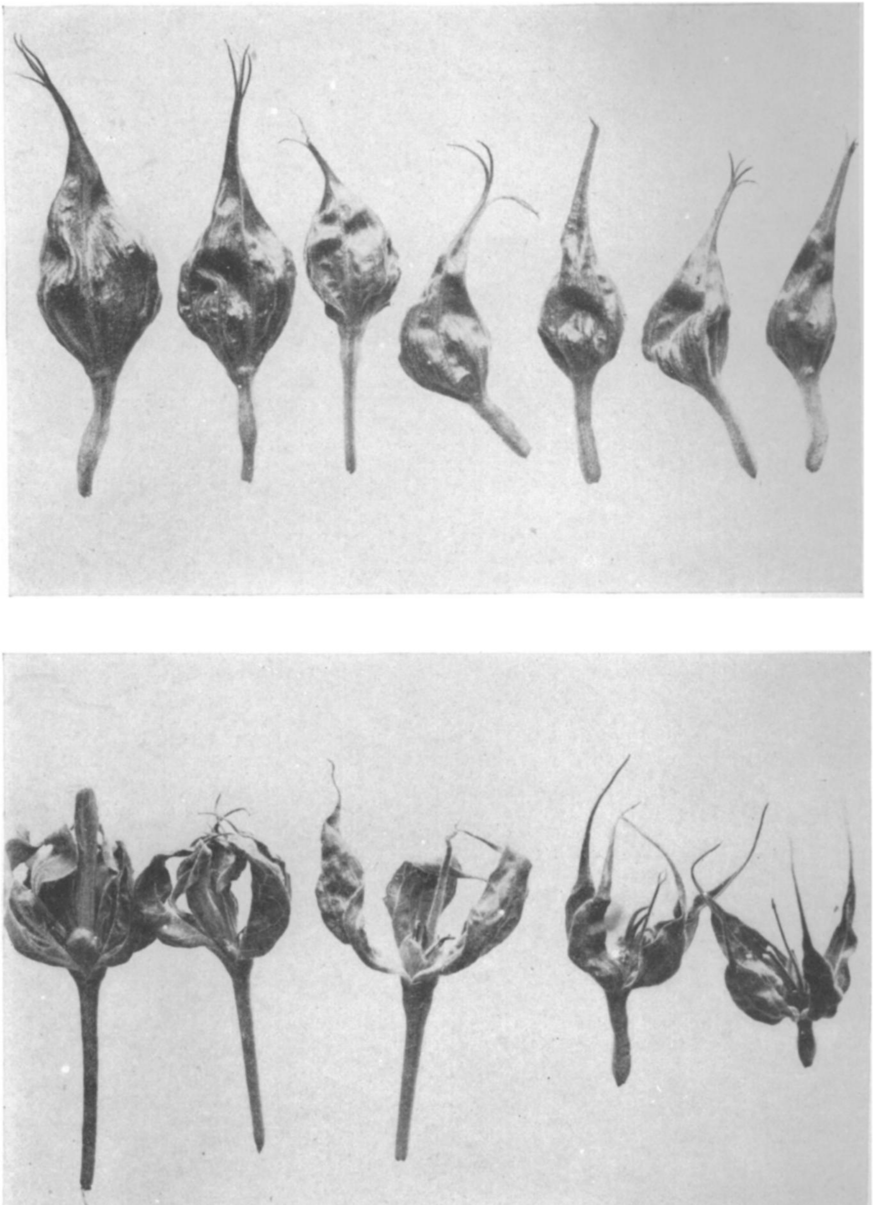
Plate 29.—Plant belonging to a race known as *Oenothera multiflora*, originally derived from the English coast near Liverpool. All but the earliest flowers are virescent or frondescent.

Plate 30.—1, Virescent buds photographed natural size, showing the peculiar baggy appearance of the calyx. 2, Virescent buds natural size, opened to show the small petals, tapering pubescent style and (buds on the left) leaves growing out from the interior.

Plate 31.—Sectorial chimera, in which the leaves on one side of the rosette are lacking in chloroplasts. In certain cases half the leaf is white and half green.



VIRESCENCE OF OENOTHERA.



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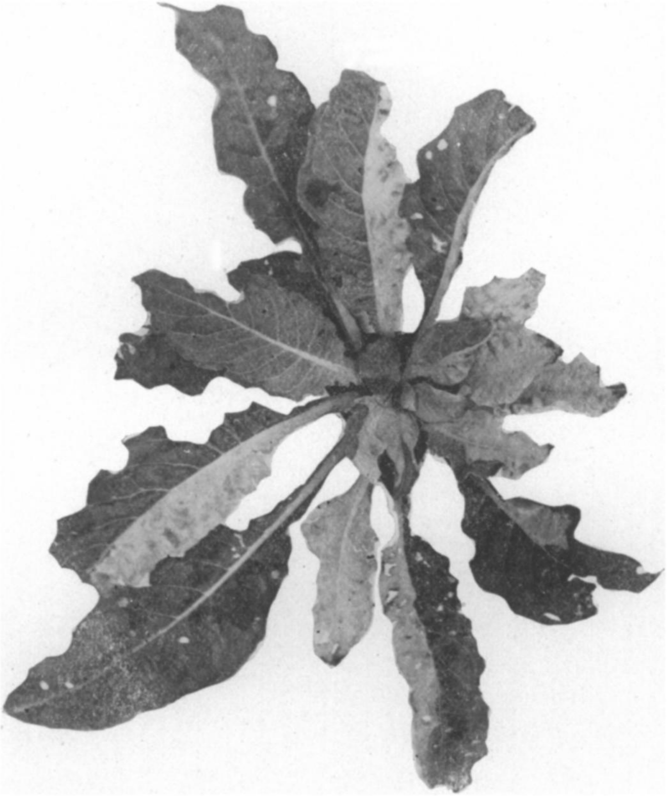

CHIMERA OF OENOTHERA.